Mar Biodiv (2017) 47:59–65
DOI 10.1007/s12526-016-0472-7

SENCKENBERG CrossMark

The invasive sun coral *Tubastraea coccinea* hosting a native Christmas tree worm at Curaçao, Dutch Caribbean

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Received: 29 December 2015 / Revised: 2 March 2016 / Accepted: 7 March 2016 / Published online: 2 April 2016

Abstract Interspecific relationships of invasive species hosting a native associated species are noteworthy, particularly if the invasive does not have a similar relationship in its native range. The azooxanthellate Indo-Pacific coral *Tubastraea coccinea* (Dendrophylliidae) has become a widespread invasive in the tropical western Atlantic, where it was probably introduced as a fouling organism in the 1930s. During recent coral reef surveys this invader has been observed as host for a native tube worm, *Spirobranchus giganteus* (Serpulidae), at Curaçao, where this association was most commonly found on a shipwreck. Although *Spirobranchus* species are known to live in association with various shallow-water corals in the Atlantic and the Indo-Pacific, none of them has been recorded as an associate of a dendrophylliid or of an azooxanthellate coral before. This new association may be possible because of the generalist host selection of *S. giganteus*, which could have been facilitated by the availability of shipwrecks and other man-made substrates.

Keywords Coral reefs · Host coral · Generalist associate · Host range · Man-made substrate · Serpulid worm

Communicated by J. D. Reimer

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Introduction

Many reports on introduced species as novel hosts for native parasites concern terrestrial ecosystems (e.g., Prider et al. 2009; Li et al. 2012; Meijer et al. 2015; Van Nieukerken and Geertsema 2015) and freshwater habitats (e.g., Glodosky and Sandland 2014; Subchev 2014). Only a few reports deal with marine host species that are recognized as invasives, and usually their parasites are co-introduced (e.g., Blakeslee et al. 2011).

Some generalist parasites are geographically widespread and already present during the introduction of the host species. For example, the American slipper limpet *Crepidula fornicata* (Linnaeus, 1758) is an introduced host for the boring sponge *Cliona celata* Grant, 1826, and the digenean trematode *Himasthla elongata* (Mehlis, 1831) in the northeastern part of the Atlantic (Hoeksema 1983; Thieltges et al. 2009), whereas both parasites also occur in their host's native range (Blakeslee et al. 2011; Carroll et al. 2015). Another example concerns ctenophores of the species *Mnemiopsis leidyi* Agassiz, 1865, which can become infested by parasitic larvae of the actiniarian genus *Edwardsiella* in the ctenophore's original native range along the North American east coast and also in its new, introduced range in northwestern Europe (Reitzel et al. 2009; Selander et al. 2010). It is difficult to find records of a marine invasive species that only hosts a particular kind of associate in its introduced range but not in its home range.

The scleractinian sun coral *Tubastraea coccinea* (Lesson, 1829) is increasingly notorious as an invasive species along the coastlines of the Caribbean, the Gulf of Mexico, and the Southwest Atlantic (Fenner and Banks 2004; Silva et al. 2014; Carlos-Júnior et al. 2015). As a native of the tropical Indo-Pacific, its occurrence in the western Atlantic was first recorded from the Caribbean islands Curaçao and Puerto Rico, where it may have been introduced in the 1930s as a fouling organism on an oil platform or a ship hull (Cairns 2000;

Fenner 2001). Boschma (1953) reported on some large *Tubastraea* corals (maximum diameter 10 cm) collected in 1948–1950 from mangrove roots, limestone, dead coral, and a ship hull in shallow water (1 m depth) at Curaçao and its neighbouring islands Bonaire and Aruba. He identified these common corals as *T. tenuilamellosa* (Milne Edwards & Haime, 1848), a junior synonym of *T. coccinea* (Cairns 2001). Roos (1971) remarked on its increasing abundance at Curaçao and its habitat expansion from shaded to more sun-exposed rocky substrates. *T. coccinea* can be considered locally harmful in its introduced range, since it has been reported to compete with the Brazilian endemic coral *Mussismilia hispida* (Verrill, 1901) (see Creed 2006) and to live as epibiont on the mussel *Perna perna* (Linnaeus, 1758), also in Brazil (Mantelatto and Creed 2015).

During a study of the host range of the Christmas tree worm *Spirobranchus giganteus* (Pallas, 1766) at Curaçao, southern Caribbean, the non-native *T. coccinea* was discovered to act as host among several other newly recorded host species. Since *T. coccinea* belongs to the scleractinian family Dendrophylliidae (Cairns 2001; Arrigoni et al. 2014), and dendrophylliid corals were unknown to host *Spirobranchus* worms, this newly discovered association is discussed from an evolutionary and ecological perspective.

Material and methods

Spirobranchus host coral surveys were performed in 2014, 2015, and 2016 during 37 dives of ~60 min each at ten localities along the leeward coast of Curaçao (Table 1). The maximum depth of most dives was 30 m, except for one (site # 3) down to 39 m. Only stony host corals were targeted, i.e., those belonging to fire corals (Hydrozoa: Anthoathecata) and scleractinians (Anthozoa: Hexacorallia). Secondary hosts overgrowing stony corals, such as octocorals and sponges (Hoeksema et al. 2015, 2016), were not included in the surveys. Both zooxanthellate and azooxanthellate scleractinian corals were examined, although azooxanthellate corals had not previously been recorded as host for *Spirobranchus* (e.g., Hunte et al. 1990; Dai and Yang 1995; Montebon and Yap 2009). Host corals were identified with the help of a field guide by Humann and DeLoach (2013).

A historical collection of 125 *Tubastraea coccinea* coral specimens (colonies and colony fragments) from Aruba (an island neighbouring Curaçao) was examined to detect a possible early representation of a *Tubastraea -Spirobranchus* association. Their maximum diameter ranges from 3 to 12 cm, with an average of 6.9 ± 2.3 (mean ± SD). The specimens are housed in the Cnidaria collection of Naturalis Biodiversity Center (catalogue nr. RMNH Coel. 3538). They were collected on 4 May 1955 from an iron beam of the wharf of Eagle Petroleum Company by Dr. P. Wagenaar Hummelinck. Most specimens have traces of iron rust on their base.

Results

During the field surveys at Curaçao, a total of 26 stony coral species were observed with associated Christmas tree worms (Table 2). The deepest record concerns a colony of *Madracis pharensis* (Heller, 1868) at 39 m depth (site 3 in Table 1). Nine of the 26 coral species represent new host records for *Spirobranchus giganteus*, whereas four previously recorded associations were not found in the present study (Table 2).

Two of the new host records concern the scleractinian family Dendrophylliidae, which previously was not known to be involved in *Spirobranchus* associations (Martin and Britayev 1998; Stella et al. 2011). These two dendrophylliid coral species, *Rhizopsammia goesi* (Lindström, 1877) and *Tubastraea coccinea* Lesson, 1829, are also the first known azooxanthellate scleractinians inhabited by *Spirobranchus. R. goesi* is uncommon in shallow water at Curaçao, where it was found in small clusters of orange corals at three of the ten survey sites (sites 4, 6, and 8 in Table 1; Fig. 1), while it was not recorded in earlier surveys at Curaçao (Roos 1971; Bak 1975; Van den Hoek et al.

Table 1 Localities at the leeward side of Curaçao where *Spirobranchus* host surveys were performed in 2014, 2015, and 2016

Locality name	Coordinates	Number of dives
1. Playa Kalki	N12°22′29″, W069°09′29″	4
2. Playa Hundu	N12°15′36″, W069°07′13″	1
3. St. Michielsbaai	N12°08′54″, W068°59′58″	2
4. Slangenbaai	N12°08′21″, W068°59′49″	1
5. Blauwbaai	N12°08′06″, W068°59′12″	5
6. Piscadera Bay (CARMABI)	N12°07′20″, W068°58′09″	9
7. Waterfactory	N12°06′34″, W068°57′16″	6
8. Megapier (with ship wreck)	N12°06′21″, W068°56′33″	2
9. Sea Aquarium	N12°04′59″, W068°53′48″	5
10. Director's Bay	N12°03′59″, W068°51′38″	2

Table 2 Coral species recorded in association with *Spirobranchus giganteus* worms at Curaçao

Species	Locality	Previous record
Class Hydrozoa, Order Anthoathecata, Suborder Capitata		
Milleporidae		
Millepora alcicornis Linnaeus, 1758	1, 3, 5, 6, 7, 8, 9	a, h
Millepora complanata Lamarck, 1816	1, 3, 4, 5, 6, 8, 9	f, g, h
Class Anthozoa, Subclass Hexacorallia, Order Scleractinia		
Acroporidae		
Acropora palmata (Lamarck, 1816)	5*, 7*	e
Agariciidae		
Agaricia agaricites (Linnaeus, 1758)	1, 3, 4, 6, 7, 9, 10	g, h
Agaricia humilis (Verrill, 1901)	3, 6, 9, 10	+
Agaricia lamarcki Milne Edwards and Haime, 1851	10	+
Astrocoeniidae		
Stephanocoenia intersepta (Lamarck, 1816)	6, 7	+
Dendrophylliidae		
Rhizopsammia goesi (Lindström, 1877)	8	+
Tubastraea coccinea Lesson, 1829	5, 6, 8, 10	+
Meandrinidae		
Dendrogyra cylindrus Ehrenberg, 1834	7, 9	+
Dichocoenia stokesii Milne Edwards and Haime, 1848	3, 6, 7, 9	d
Eusmilia fastigiata (Pallas, 1766)	3, 7	g
Meandrina meandrites (Linnaeus, 1758)	6	+
Merulinidae		
Orbicella annularis (Ellis and Solander, 1786)	1, 3, 4, 5, 6, 7, 9	d, e, f, g, h
Orbicella faveolata (Ellis and Solander, 1786)	3, 4, 5, 6, 9	+
Orbicella franksi (Gregory, 1895)	4, 5, 6, 7, 9	+
Montastraeidae		
Montastraea cavernosa (Linnaeus, 1767)	3, 7, 9, 10	d, f, g, h
Mussidae		
Colpophyllia natans (Houttuyn, 1772)	5, 6, 7, 8, 9	d
Diploria labyrinthiformis (Linnaeus, 1758)	3, 5, 6	a, g
Pseudodiploria strigosa (Dana, 1846)	1, 3, 4, 5, 6, 7, 9, 10	b, d, e, f, h
Oculinidae		
Oculina valenciennesi Milne Edwards and Haime, 1850		b**
Pocilloporidae		
Madracis auretenra Locke, Weil and Coates, 2007	3, 4, 5, 6, 7, 9	d***, e***
Madracis decactis (Lyman, 1859)	3, 5, 6	e
Madracis formosa Wells, 1973		e
Madracis pharensis (Heller, 1868)	3	c
Poritidae		
Porites astreoides Lamarck, 1816	1, 2, 3, 4, 5, 6, 7, 9, 10	d, e, f, g, h
Porites branneri Rathbun, 1887		e
Porites furcata Lamarck, 1816		e
Porites porites (Pallas, 1766)	3, 5, 6, 9	d, e, f
Siderastreidae		
Siderastrea siderea (Ellis and Solander, 1768)	3, 5, 6, 7, 9, 10	d****, e, f, g, h

Locality numbers refer to sites mentioned in Table 1. New host records are marked by +. Previous host records are from Curaçao by (a) Pallas (1766), (b) Ten Hove (1970), (c) Steward-Van Es (1978), (d) Reuvekamp (1989); from Jamaica by (e) Scott (1987); from Barbados by (f) Hunte et al. (1990); from Cozumel, Mexico by (g) Petitjean and Myers (2005); from Bonaire by (h) Nygaard (2008). * association with *Spirobranchus polycerus* (Schmarda, 1861); ** species identification added by Roos (1971); *** recorded as *Madracis mirabilis* (Duchassaing and Michelotti, 1860); **** recorded as *Siderastrea radians* (Pallas, 1766)

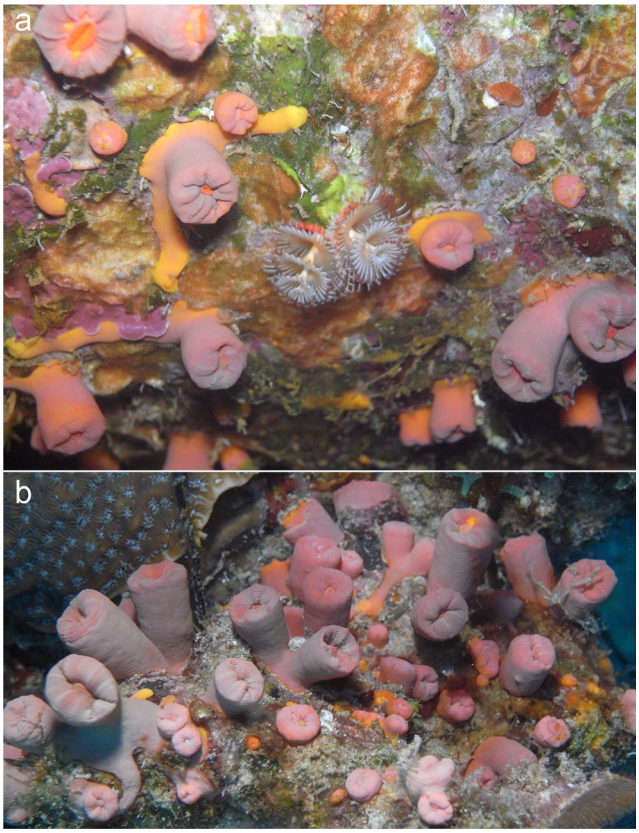

Fig. 1 *Rhizopsammia goesi* corals at two sites on Curaçao. **a** With a *Spirobranchus giganteus* worm on the hull of the shipwreck "Superior Producer" next to the Mega Pier, ca. 23 m depth. **b** Without *Spirobranchus* underneath an overhang at CARMABI, Piscadera Bay, ca. 15 m depth

1978). At only one of these three localities, *Rhizopsammia* was found in association with *Spirobranchus*, on the hull of a ship wreck where a single serpulid worm was found surrounded by several coral polyps (Table 2; Fig. 1a).

At four survey sites, corals of the invasive *Tubastraea coccinea* were observed with associated *Spirobranchus* worms (Fig. 2). It was difficult to quantify this association (as proportion of corals with worms) because the *Tubastraea* corals formed dense aggregations in which many colonies appeared to be fused or growing on top of each other, and therefore could not be clearly distinguished as separate units. At three of these four sites (sites 5, 6, and 10 in Table 1) this association was found at 1–2 m depths.

None of the *Tubastraea* specimens collected in 1955 from Aruba had remnants of *Spirobranchus* tubes on them. Hence, there is no proof yet that Christmas tree worms were previously associated with *T. coccinea* since its introduction in the Caribbean. Several of the old coral specimens had empty tubes of the serpulids *Vermiliopsis annulata* (Schmarda, 1861) and *Hydroides* sp. attached to their base, where the corals were connected to their metal substrate.

Discussion

The association of the invasive *Tubastraea coccinea* with the native *Spirobranchus giganteus* is remarkable, because *T. coccinea* and other dendrophylliid coral species were unknown as hosts for *Spirobranchus* worms, which includes their Indo-Pacific home range. The association of native *Rhizopsammia* and *Spirobranchus* species is of interest from an evolutionary perspective, since corals of the dendrophylliid genera *Rhizopsammia* and *Tubastraea* show strong morphological resemblances (Figs. 1 and 2), whereas they are closely but not directly related from a phylogenetic point of view (Cairns 2001; Arrigoni et al. 2014). These two dendrophylliids also represent the first records of azooxanthellate corals hosting *Spirobranchus*. Corals of both host species do not appear to overgrow the worm tubes (Figs. 1 and 2), and therefore the latter seem to function more as epifauna than as endofauna, whereas *Spirobranchus* worms in many other scleractinians become predominantly covered by coral tissue, with the exception of the tube opening (Nishi and Nishihira 1996; Hoeksema and Ten Hove 2014). The striking occurrence of *S. giganteus* in its new host, as well as in many other coral species, indicates that this tube worm is a generalist in its host selection, and perhaps more so than its congeners in the Indo-Pacific, which have not yet been observed to inhabit dendrophylliids.

In addition to the invasive *Tubastraea coccinea*, eight native coral species also represent new host records for *Spirobranchus* in the present study (Table 2), whereas several other Atlantic coral species have not yet been reported as hosts, such as those belonging to seven out of ten genera of the scleractinian family Mussidae (Budd et al. 2012): *Favia*, *Isophyllia*, *Manicina*, *Mussa*, *Mussismilia*, *Mycetophyllia*, and *Scolymia*. The cause for this restricted representation of mussid corals among a total of 30 recorded *Spirobranchus* hosts (Table 2) is unclear, all the more so because a similar host selection is not shown by Atlantic gall crabs (Van der Meij 2014).

In general, some Indo-Pacific *Spirobranchus* worms also appear to be generalists (Dai and Yang 1995; Montebon and Yap 2009), and one species is even able to settle on non-coral hosts, such as giant clams (Van der Schoot et al. 2016). Because the present report contains nine new host records for just the Caribbean, surveys are needed in other coral reef areas in order to obtain a more complete overview of host corals for *Spirobranchus*. This would provide a better overview of phylogenetic relationships of coral species acting as *Spirobranchus* hosts, as shown for various associates of mushroom corals (Fungiidae) in the Indo-Pacific (Hoeksema et al. 2012; Van der Meij et al. 2015).

The absence of known *Spirobranchus-Tubastraea* associations in the Indo-Pacific does not imply that the latter have no associated fauna in their native range. *Tubastraea* species in the Indo-Pacific are commonly under attack from

Fig. 2 *Tubastraea coccinea* corals with associated *Spirobranchus giganteus* at three sites on Curaçao. **a–g** On the superstructure and hull of the shipwreck "Superior Producer" next to the Mega Pier, 15–25 m depth. **h** Underneath an overhang at CARMABI, Piscadera Bay, ca. 1 m depth. **i** Underneath an overhang in Director's Bay, ca. 2 m depth

corallivorous wentletrap snails (Epitoniidae: *Epidendrium* spp.), which consume soft coral tissue from the coral calices and are known to occur from the Red Sea to the Pacific coast of Central America (Gittenberger and Gittenberger 2005; Rodríguez-Villalobos et al. 2016), while they can also host coral-dwelling barnacles (Gittenberger and Hoeksema 2013: Figs. 3–4). Because these epitoniid snails are generally host-specific (Gittenberger and Gittenberger 2005; Gittenberger and Hoeksema 2013) and unknown to be co-introduced parasites along with their hosts, it is unlikely that epitoniids will attack *Tubastraea* corals in the Atlantic. Another predator of *Tubastraea* species, the nudibranch *Phestilla melanobranchia* Bergh, 1874, has been reported from Singapore to Hawaii (Harris 1975; Faucci et al. 2007), but so far not from the Atlantic.

The highest abundances of *Tubastraea* corals and *Tubastraea*-associated *Spirobranchus* worms were encountered on a shipwreck. The historical collection of *T. coccinea* from Aruba was also sampled from artificial (metal) substrate in a ship wharf. *Tubastraea* corals appear to settle and grow readily on man-made substrates, which so far has been most clearly shown in the Atlantic (Creed and de Paula 2007; Shearer 2009; Moreira et al. 2014) but since recently also in the Indo-Pacific (Ho et al. 2016). Since *Tubastraea* species in the western Atlantic were most likely introduced and dispersed as fouling organisms (Cairns 2000; Fenner 2001; Ferreira 2003; Fenner and Banks 2004), the availability of man-made substrate may be helpful in maintaining its population and also its association with *S. giganteus*.

Acknowledgments We thank staff of CARMABI and Curaçao Sea Aquarium for their hospitality and logistic support. We are also grateful to Antonio Baeza, Gerhard C. Cadée, Marco Faasse, Charles H.J.M. Fransen, Ton van Haaren, André Klicpera, Otto Moog, Godfried W.N.M. van Moorsel, Julian D. Reynolds, Menno Schilthuizen, and Erik J. van Nieukerken for discussions on introduced host species through ResearchGate. We thank two anonymous reviewers for their constructive comments. This publication is Ocean Heritage Foundation / Curaçao Sea Aquarium / Substation Curaçao (OHF/ CSA/SC) contribution number 23.

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